

NEW PALAEOMACROMIID DRAGONFLIES FROM THE UPPER PALEOCENE OF ARGENTINA

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ABSTRACT. A new genus of palaeomacromiid dragonflies, *Curviarculia*, based on *Curviarculia delicata* sp. nov. and *Curviarculia lamasi* sp. nov., is erected from the upper Paleocene Maíz Gordo Formation of north-western Argentina. Phylogenetic relationships within Palaeomacromiidae are discussed, leading to a new family diagnosis.

KEY WORDS. Insecta, Odonata, Palaeomacromiidae, gen. et sp. nov., phylogeny, Paleocene, Argentina.

THE fossil family Palaeomacromiidae Petrulevicius *et al.*, 1999 was previously known as a monospecific taxon (Petrulevicius *et al.* 1999) from the Maíz Gordo Formation, a late Paleocene (Volkheimer *et al.* 1984; Marshall *et al.* 1997; Quattrocchio *et al.* 1997) lacustrine sequence that crops out in north-west Argentina (del Papa and Marquillas 1990). The discovery of two new species belonging to a new genus, *Curviarculia*, provides more information about this fragmentary and unique taxon. These are the second and third species of Palaeomacromiidae to be described.

The specimens studied were collected from the Maíz Gordo Formation. *Curviarculia delicata* gen. et sp. nov. and *Palaeomacromia multicellulata* Petrulevicius *et al.*, 1999 were recovered from the same locality. It is 6 km south-west of the village of La Mendieta, at 24° 21' S, 64° 59' W, in the province of Jujuy (north-west Argentina) (Text-fig. 1A). The section is composed of red and green siltstone, yellow and green shales, and stromatolitic boundstone (Text-fig. 1B). At the top of the section, Quaternary sediments rest unconformably on the Maíz Gordo Formation. This succession was deposited beyond the western boundary of the Salta-Jujuy High (see Text-fig. 1A). Green shale and stromatolitic boundstone facies indicate a carbonate mudflat environment interpreted as a period of high-stand water-depth (green shales), and progressively shallower water with stromatolitic boundstone formation (del Papa 1999). *Curviarculia lamasi* sp. nov. was collected from a section 235 m thick, measured by del Papa (1994). The locality is in El Garabatal creek, Santa Bárbara Range, at 24° 16' S, 64° 25' W, in the province of Jujuy. The sediments were deposited on the south-west margin of the Lomas de Olmedo depocenter (Salfity and Marquillas 1994). The fossiliferous strata are composed of calcareous couplets within the lower third of the formation, 95 m above the base of the section (see del Papa 1994). These carbonate laminites are interpreted as having formed in a stable, chemically stratified water body of meromictic type, at an internal lake position (del Papa 1999; Petrulevicius 2001). Both findings come from spatially related subenvironments of the same lake (see del Papa 1999). The lateral association of these facies depends on stratigraphic and geographic positions that in this case do not contradict the contemporaneity of both finds.

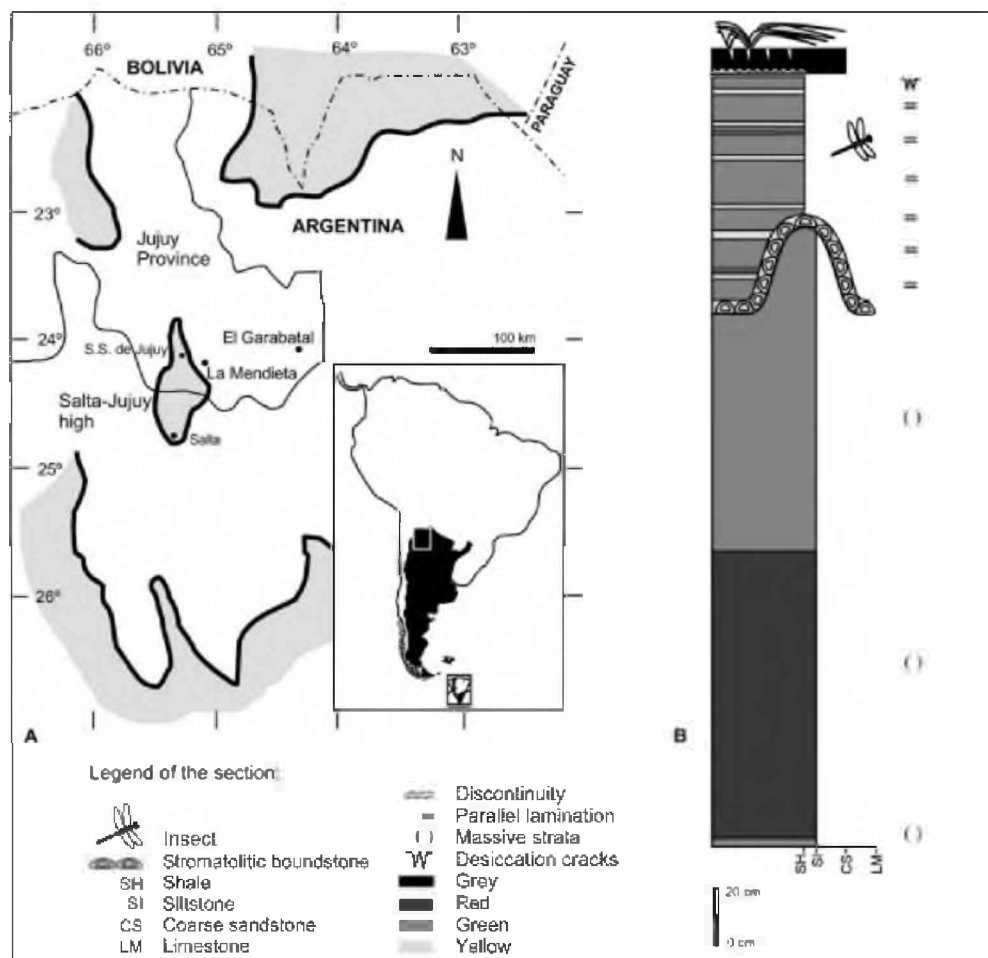
In the systematic section below, we use the wing venation nomenclature of Riek (1976), and Riek and Kukalová-Peck (1984), as amended by Kukalová-Peck (1991), Nel *et al.* (1993) and Bechly (1995, 1996). We follow the phylogenetic classification of Anisoptera proposed by Bechly (1996), as subsequently amended (Bechly, 1997).

SYSTEMATIC PALAEONTOLOGY

ODONATA Fabricius, 1793

ANISOPTERA Selys, 1854

PALAEOMACROMIIDAE Petrulevicius, Nel and Muzón, 1999



TEXT-FIG. 1. Location of La Mendieta and El Garabatal exposures and stratigraphy of the Maiz Gordo Formation study-section at La Mendieta, Jujuy. A, palaeogeographical map of Santa Bárbara Subgroup, redrawn from Salfity and Marquillas (1994) and del Papa (1999). Structural highs are indicated by shading; B, section at La Mendieta.

Type genus. *Palaeomacromia* Petrulevicius, Nel and Muzón, 1999.

Phylogenetic definition. Palaeomacromiidae shall include all dragonflies that are more closely related to *Palaeomacromia multicellulata* Petrulevicius *et al.*, 1999 than to any of the type species of the other type genera of the Anisoptera family-group taxa *sensu* Fraser (1957) (stem-based definition).

Emended diagnosis. The main venational characters of this family are as follows: (1) discoidal triangle divided into numerous (6?–8) cells; (2) subtriangle divided into numerous (5–7) cells; (3) median and submedian spaces free of crossveins; (4) no bridge-crossveins; (5) primary antenodals distinctly stronger than the numerous secondaries; (6) RP3/4 and MA distally undulate; (7) ‘cordulegasterid’ and ‘libellulid’ gaps present for a long distance basal and distal of the subnodus; (8) Rspl and Mspl distinct; (9) two rows of cells between Rspl and IR2; (10) area between IR2 and RP2 greatly widened distally; (11) the anal area between AA and posterior wing margin is very broad, with five rows of cells; (12) CuA has no strong posterior branches; (13) postdiscoidal area very broad, with five rows of cells between MA and MP; (14)

CuP placed between the two primary antenodals; (15) the basal first secondary antenodal of the second row between ScP and RA absent; (16) first postnodal between ScP and RA is developed as 'palaeomacromiid' oblique vein. Character states 1, 2 and 10–16 are autapomorphies of Palaeomacromiidae; character states 2 and 10–13 are convergently present in some Libellulidae but strictly absent in more basal Italoansida Bechly, 1996.

Remarks. *Curviarculia delicata* sp. nov. and *Curviarculia lamasi* sp. nov. contribute to the variability of the family Palaeomacromiidae, i.e. subtriangle divided into six (the former) to seven (the latter) cells, quadrilateral hypertriangle with two crossveins, and interspace between RP1 and RP2 stays unicellular for four cells in *Curviarculia lamasi*. With the discovery of these two species, new synapomorphies of Palaeomacromiidae have been recognized and formulated: (1) CuP placed between the two primary antenodals; (2) the basal first secondary antenodal of the second row between ScP and RA absent; (3) first postnodal between C and RA is developed as a 'palaeomacromiid' oblique vein.

Genus CURVIARCULIA gen. nov.

Derivation of name. After presence of curved arcus.

Type species. *Curviarculia delicata* gen. et sp. nov.

Phylogenetic definition. *Curviarculia* shall include all dragonflies that are more closely related to *Curviarculia delicata* than to any of the other type species of the other type genera of the Anisoptera family-group taxa *sensu* Fraser (1957) (stem-based definition).

Included taxa. *Curviarculia delicata* sp. nov. and *Curviarculia lamasi* sp. nov.

Diagnosis. The main venational characters of this genus are as follows: (1) subtriangle divided into more (6–7) cells than in *Palaeomacromia*; (2) quadrilateral hypertriangle, not triangular as in *Palaeomacromia*; (3) hypertriangle crossed by two crossveins, as opposed to free in *Palaeomacromia*; (4) curved arcus with an extremely short posterior portion, not straight as in *Palaeomacromia*.

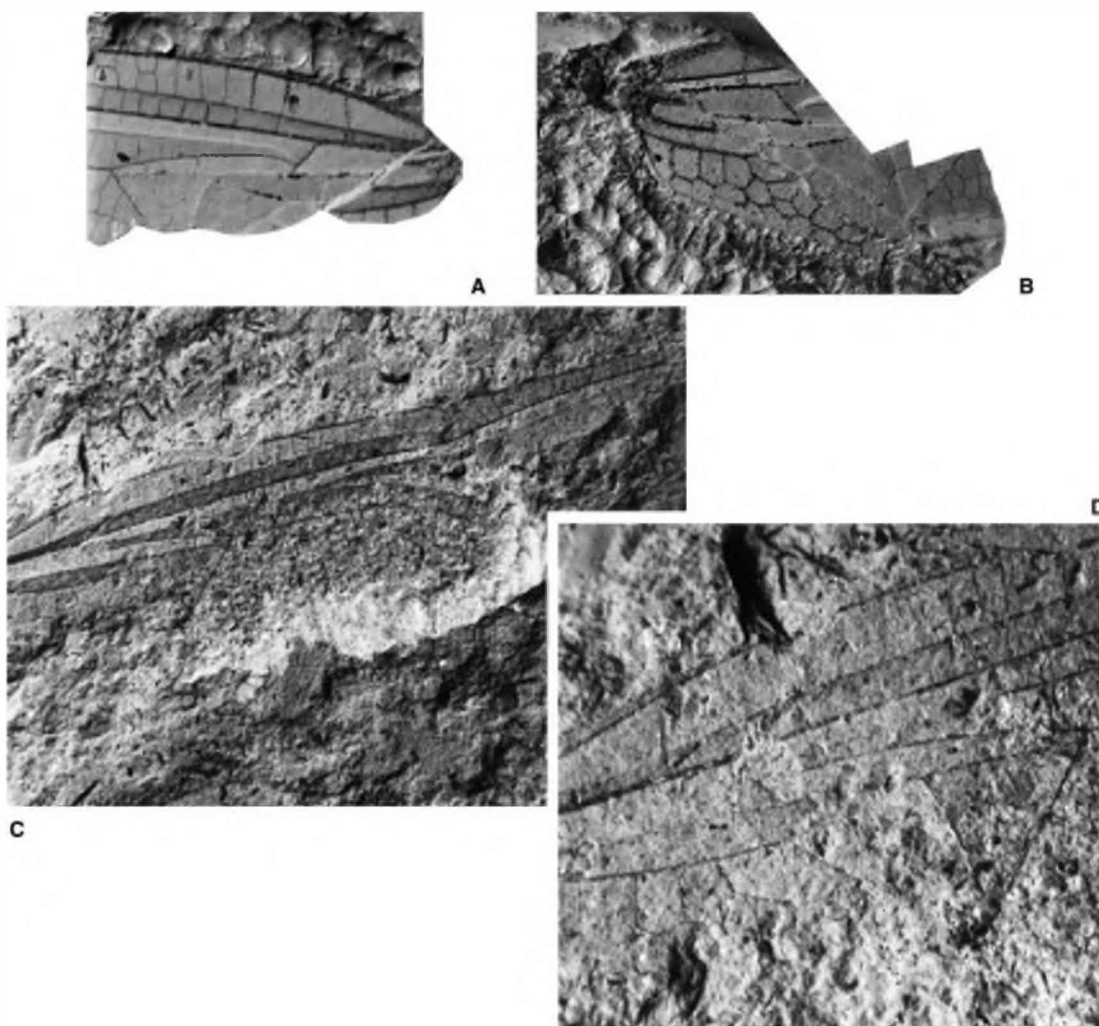
Remarks. Based on the systematics of Palaeomacromiidae (Petrulevicius *et al.* 1999) and on the phylogenetic system of Anisoptera proposed by Bechly (1996, 1997), we justify the erection of a new genus. *Curviarculia* shares with *Palaeomacromia* Petrulevicius *et al.*, 1999 the presence of five synapomorphies: (1) discoidal triangle divided into numerous (eight) cells; (2) postdiscoidal area very broad, with four (*Curviarculia delicata*) to five (*Curviarculia lamasi*) rows of cells between MA and MP; (3) subtriangle divided into numerous (five to seven) cells; (4) CuP placed between the two primary antenodals; (5) first postnodal between ScP and RA is developed as 'palaeomacromiid' oblique vein. Other characters of Palaeomacromiidae are not preserved (see Petrulevicius *et al.* 1999). *Curviarculia* differs from *Palaeomacromia* in the character states listed in the generic diagnosis. Nevertheless, the polarisation of these characters remains difficult to establish because the relationships of Palaeomacromiidae within Italoansida remain uncertain.

Curviarculia delicata sp. nov.

Text-figures 2–3

Derivation of name. After the delicate nature of the specimen.

Holotype. Specimen MLP 28865 (part and counterpart), in the Departamento Científico Paleozoología Invertebrados, Museo de la Plata, Argentina.



TEXT-FIG. 2. A, *Curviarculia delicata* sp. nov., MLP 28865 (holotype), La Mendieta, province of Jujuy, north-west Argentina; Maíz Gordo Formation, late Palaeocene, counterpart; $\times 3.6$. B, *Curviarculia delicata* sp. nov., MLP 28865 (holotype), part; $\times 3.9$. C, *Curviarculia lamasi* sp. nov., Departamento Científico Paleozoología Invertebrados, MLP 28157 (holotype); El Garabatal, province of Jujuy, north-west Argentina; Maíz Gordo Formation, late Paleocene; forewing, $\times 3.2$. D, *Curviarculia lamasi* sp. nov., (holotype), base of forewing, detail; $\times 7.3$.

Type locality and horizon. La Mendieta, province of Jujuy, north-west Argentina, latitude $24^{\circ} 21' S$, longitude $64^{\circ} 59' W$, Maíz Gordo Formation, late Palaeocene (Volkheimer *et al.* 1984; Marshall *et al.* 1997; Quattrocchio *et al.* 1997).

Diagnosis. The main venational characters of this species are as follows: (1) subtriangle divided into six cells, instead of seven in *C. lamasi*; (2) postdiscoidal area less broad than in *C. lamasi*, with four rows of cells between MA and MP.

Description. Print of the basal one-quarter of a forewing, no trace of coloration preserved. Length of the preserved part 14 mm; width 9.4 mm. Eight secondary antenodal crossveins preserved distal of Ax_2 , not aligned with those of the second row between ScP and RA; last four with two crossveins 8-shaped. Vein Ax_0 partly preserved at wing base (between costal margin and ScP). Primary antenodals (Ax_1 , Ax_2) distinctly stronger than others. No secondary

antenodal crossvein between the two primaries and basal of Ax_1 . Six preserved crossveins in area between RA and RP. Discoidal triangle eight-celled, transverse; length of its anterior side 3.4 mm; distal side 3.5 mm; basal side 3.22 mm. Supratriangle long and with two crossveins, quadrilateral in shape. Median and submedian cells free of crossveins. CuP 1.4 mm basal of level of arculus. RP and MA meeting at their very base in arculus. Arculus slightly curved, with its posterior part distinctly shorter than its anterior part. Arculus midway between primary antenodal crossveins. A well-defined PsA forms an angle (anterior 20 degrees) with basal part of AA, separating a large six-celled subtriangle; length of its anterior side 2.6 mm; distal side 3.1 mm; basal side 4.3 mm, more or less triangular in shape. Anal area very wide, with three or four rows of cells between AA and posterior wing margin. CuA weak with no well-defined posterior branches. Six rows of cells in cubito-anal area. Postdiscoidal area with four rows of cells just distal of discoidal triangle (3.22 mm wide).

Remarks. *C. delicata* has four of the synapomorphies of the Palaeomacromiidae, i.e. discoidal triangle divided into numerous (eight) cells; subtriangle divided into numerous (5–7) cells; postdiscoidal area very broad, with 4–5 rows of cells between MA and MP; CuP placed between the two primary antenodals. Other characters of the Palaeomacromiidae are not preserved (Petrulevicius *et al.* 1999). *C. delicata* differs from *C. lamasi* in the presence of a subtriangle divided into six cells, a postdiscoidal area with four rows of cells between MA and MP, and the PsA forming an angle (anterior 20 degrees) with the basal part of AA. Both species share the presence of curved arculus and quadrangular hypertriangle with two crossveins; which justifies their inclusion in a new genus.

Curviarculia lamasi sp. nov.

Text-figures 2–3

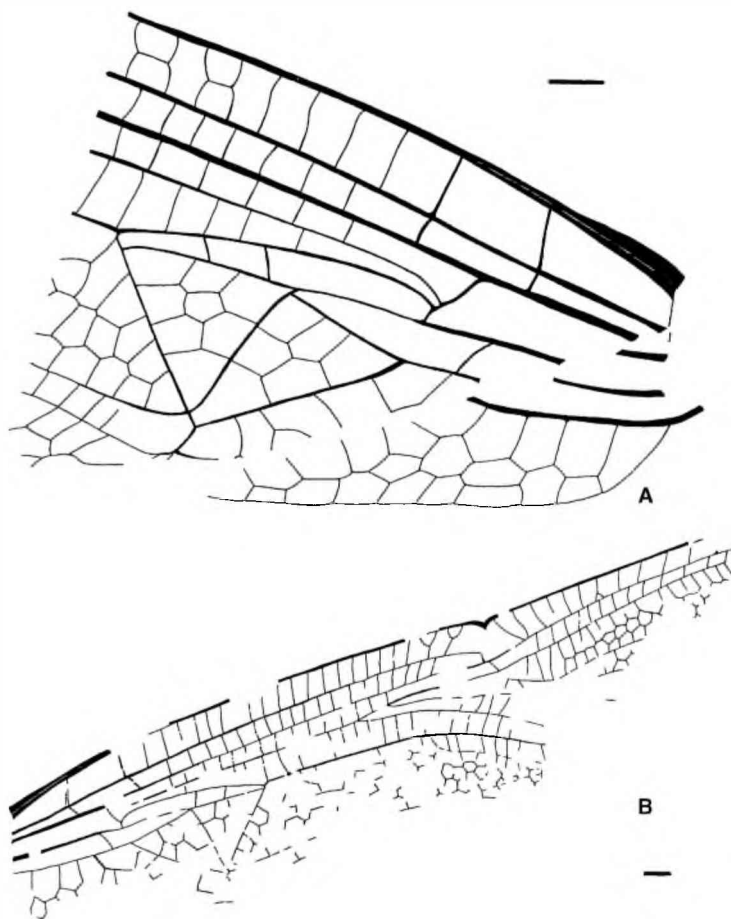
Derivation of name. After the north-western gaucho Mr Domingo Lamas, friend from El Fuerte, whose hospitality made possible the first author's survival in the Santa Bárbara mountains.

Holotype. Specimen MLP 28866 (counterpart), in the Departamento Científico Paleozoología Invertebrados, Museo de la Plata, Argentina.

Type locality and horizon. El Garabatal, province of Jujuy, north-west Argentina, latitude 24° 16' S, longitude 64° 25' W, Maíz Gordo Formation, late Paleocene (Volkheimer *et al.* 1984; Marshall *et al.* 1997; Quattrocchio *et al.* 1997).

Diagnosis. The main venational characters of this genus are as follows: (1) subtriangle divided into seven cells, instead of six in *C. delicata*; (2) curved arculus with an extremely short posterior portion; (3) postdiscoidal area very broad, with five rows of cells between MA and MP; (4) first postnodal vein strongly distally arched (character unknown in *C. delicata*).

Description. Print of the basal four-fifths of a forewing, no trace of coloration preserved. Length of preserved part 32.8 mm; probable length of wing *c.* 40 mm; width 7.5 mm. Distance from base to nodus 19.7 mm; from arculus to nodus 15.5 mm. Only base of basal vein of pterostigma preserved. Eleven postnodal crossveins, not aligned with corresponding postsubnodal crossveins between RA and RP1, the seventh being Y-shaped. One preserved crossvein below the pterostigma. First postnodal vein strongly oblique. The basal first postsubnodal crossveins absent ('libellulid gap' present). Twenty-two secondary antenodal crossveins between arculus and nodus, distal of Ax_2 , not aligned with those of second row between ScP and RA, the last two being Y-shaped. Most distal antenodal crossvein of second row absent. Primary antenodals distinctly stronger than others. No secondary antenodal crossvein between two primaries and basal of Ax_1 . Fifteen crossveins in area between RA and RP basal of RP3/4 but none between base of RP3/4 and subnodus ('cordulegastrid gap' present). No bridge-crossveins (Bqs) preserved, except one close to oblique crossvein 'O'. Discoidal triangle 6–8?-celled, transverse; length of its anterior side 2.94 mm; distal side 3.5 mm; basal side 2.8 mm. Supratriangle long with two crossveins. Median and submedian cells free of crossveins. CuP 1.02 mm basal of level of the arculus. MA meets at their very base in arculus. Curved arculus, with an extremely short posterior portion, which is in consequence mainly formed by RP+MA. Arculus midway between the two primary antenodal crossveins. A well-defined PsA aligned with basal part of AA, separating a large seven-celled subtriangle; length of its basal side 3.9 mm; anterior side 2.6 mm; distal side 2.91 mm, more or less triangular in shape. Anal area very wide, with two or



TEXT-FIG. 3. A, *Curviarculia delicata* sp. nov., MLP 28866 (holotype), La Mendieta, province of Jujuy, north-west Argentina; Maíz Gordo Formation, late Paleocene, forewing reconstruction; scale bar represents 1 mm. B, *Curviarculia lamasi* sp. nov., Departamento Científico Paleozoología Invertebrados, MLP 28157 (holotype), El Garabatal, province of Jujuy, north-west Argentina, Maíz Gordo Formation, late Paleocene, forewing reconstruction; scale bar represents 1 mm.

more rows of cells between AA and posterior wing margin. CuA weak. Five or six rows of cells in cubito-anal area. Postdiscoïdal area with five or six rows of cells just distal to discoïdal triangle (2.8 mm wide), not distinctly broader along posterior wing margin. Mspl seems to be well defined but parallel with MA, with one row of cells between it and MA. MA and RP3/4 parallel; both seem to be distinctly undulate somewhat distal of nodus. RP2 originating at subnodus. Anterior preserved part of an oblique crossvein 'O' 1 mm distal of subnodus. 'Libellulid oblique vein' absent in area between RP1 and RP2. IR2 gently curved. RP2 more undulate. Two rows of cells between IR2 and RP2 4.7 mm distal of subnodus, well basal of level of pterostigma. Rspl seems to be well defined. Interspace between RP1 and RP2 stays unicellular for four cells and distally more than four rows of cells between RP1 and RP2. Possible presence of straight IR1 between RP1 and RP2.

Remarks. *C. lamasi* has five of the synapomorphies of the Palaeomacromiidae: (1) discoïdal triangle divided into numerous (eight) cells; (2) subtriangle divided into numerous (5–7) cells; (3) postdiscoïdal area very broad, with five rows of cells between MA and MP; (4) CuP placed between the two primary

antenodals; (5) area between IR2 and RP2 greatly widened distally. Other characters of *Palaeomacromiidae* are not preserved (Petrulevicius *et al.* 1999). *C. lamasi* is not related to *Palaeomacromia* because of its subtriangle, which is divided into seven cells, its curved arcus, its quadrangular hypertriangle with two crossveins, and because of the presence in *Palaeomacromia* of fewer secondary antenodal crossveins of the second row between ScP and RA than in *C. lamasi*.

CONCLUSIONS

The *Palaeomacromiidae* was until now a monospecific taxon (Petrulevicius *et al.*, 1999). The discovery of two more species increases the morphological variability of the taxon, and allows the recognition of synapomorphies within two hierarchical levels of taxa included in the monophylum. Unfortunately, because of the fragmentary state of the specimens, these findings do not add new information on the phylogenetic relationships of the taxon within the Italoansida.

The discovery of two species of *Curviarculia*, in addition to *Palaeomacromia multicellulata*, demonstrates an important diversity of palaeomacromiids during the deposition of the fossil-bearing strata. The distribution of the representatives of the family is restricted, so far, to the Lomas de Olmedo depocenter *sensu* Salfity and Marquillas (1994). It is rather surprising that this family is still unknown in the Upper Cretaceous and in other Paleogene deposits.

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